

The University of Chicago

AUTONOMIC AND MOTOR LOCALIZA-
TION IN THE HYPOTHALAMUS

A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF THE
BIOLOGICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF PHYSIOLOGY

1937

By

NORRIS L BROOKENS

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AUTONOMIC AND MOTOR LOCALIZATION IN THE HYPOTHALAMUS

NORRIS L BROOKENS, PH.D.

CHICAGO

Present knowledge of the function of the hypothalamic regions has been obtained in various ways. Destruction of localized areas within the hypothalamus has demonstrated centers for: water balance (Bailey and Bremer;¹ Camus and Roussy;² Fisher, Ingram and Ranson³); carbohydrate metabolism (Davis, Cleveland and Ingram;⁴ Roussy and Mosinger⁵); the rhythm of sleep (Hess;⁶ Ranson and Ingram⁷), and regulation of body temperature (Ranson and Ingram;⁸ Isenschmidt and Schnitzler⁹). The presence of a sleep center here was first indicated by the anatomic and pathologic studies of von Economo¹⁰ (1930). Bard¹¹ compared the behavior of hypothalamic cats, with the cortex and thalamus removed, and that of decerebrate cats in which the hypothalamus in addition had been removed and showed that the hypothalamus is a center for manifestation of the emotions, particularly rage.

From the Department of Physiology, the University of Chicago.

1. Bailey, P., and Bremer, F.: Experimental Diabetes Insipidus, *Arch. Int. Med.* **28**:773 (Dec.) 1921.
2. Camus, J., and Roussy, G.: *J. de physiol. et de path. gén.* **20**:509, 1922.
3. Fisher, C.; Ingram, W. R., and Ranson, S. W.: Relation of Hypothalamico-Hypophyseal System to Diabetes Insipidus, *Arch. Neurol. & Psychiat.* **34**:124 (July) 1935.
4. Davis, L.; Cleveland, D., and Ingram, W. R.: Carbohydrate Metabolism: Effect of Hypothalamic Lesions and Stimulation of Autonomic Nervous System, *Arch. Neurol. & Psychiat.* **33**:592 (March) 1935.
5. Roussy, G., and Mosinger, M.: *Ann. de méd.* **33**:193, 1933.
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7. Ranson, S. W., and Ingram, W. R.: *Am. J. Physiol.* **101**:690, 1932.
8. Ranson, S. W., and Ingram, W. R.: *Proc. Soc. Exper. Biol. & Med.* **32**:1439, 1935.
9. Isenschmidt, R., and Schnitzler, W.: *Arch. f. exper. Path. u. Pharmacol.* **76**:202, 1914.
10. von Economo, C.: *J. Nerv. & Ment. Dis.* **71**:249, 1930.
11. Bard, Philip: *Am. J. Physiol.* **84**:490, 1928.

Stimulation (Karplus and Kreidl¹²) demonstrated an orthosympathetic center in the hypothalamus, for from it are obtained such typical sympathetic reactions as pupillary dilatation, increase in the blood pressure and respiration and pilomotor contraction; the presence of parasympathetic centers is indicated as well, for Beattie and his co-workers¹³ found increased motor activity of the stomach and intestines and cardiac arrhythmia with no modification in respiratory rate and, more recently,¹⁴ an increase (and also a decrease) in bladder tone. Separate representation in the hypothalamus of the two parts of the autonomic system (Cushing¹⁵) is only roughly established; indeed, sleep has been produced by stimulation (Hess⁶) and by destruction (Ranson and Ingram⁷) of supposedly the same hypothalamic region. Perhaps the discordance of results is due to the difficulty in reaching this region of the brain.

Karplus and Kreidl¹² stimulated the rough surface of the hypothalamus, exposed by various transverse sections, while Ranson and his co-workers¹⁶ used the Horsley-Clarke apparatus. With this instrument, extensive exploration was made of points influencing blood pressure, respiration and bladder tone. Both groups of investigators concluded that the hypothalamus is only an orthosympathetic center, but emphasized the possibility of the passage of parasympathetic tracts through the area. Beattie and his co-workers^{13a} stimulated the wall of the third ventricle but, unfortunately, did not describe their method, nor can one accurately interpret the drawings. Their experiments indicated a parasympathetic center in the hypothalamus.

The motor part of the frontal lobe has been shown also to be sympathicomotor. Stimulation of certain areas here results in increased blood pressure (Hoff and Green¹⁷), and extirpation of the frontal lobe leads to disturbances in vasomotor control and in gastro-intestinal movements (Fulton, Kennard and Watts¹⁸). There is also evidence of a sympathicosensory function in this region (Dusser de Barenne¹⁹).

12. Karplus, J. P., and Kreidl, A.: *Arch. f. d. ges. Physiol.* **215**:667, 1927.

13. (a) Beattie, J.; Brow, G. P., and Long, C. H.: *A. Research Nerv. & Ment. Dis., Proc.* **9**:249, 1930. (b) Beattie, J.: *Canad. M. A. J.* **26**:278, 1932.

14. Beattie, J., and Kerr, A. S.: *Brain* **59**:302, 1936.

15. Cushing, H.: *Papers Relating to the Pituitary Body, Hypothalamus and Parasympathetic System*, Springfield, Ill., Charles C. Thomas, Publisher, 1932.

16. (a) Ranson, S. W.; Kabat, H., and Magoun, H. W.: *Am. J. Physiol.* **109**: 85, 1934; (b) *Autonomic Responses to Electrical Stimulation of Hypothalamus, Preoptic Region and Septum*, *Arch. Neurol. & Psychiat.* **33**:467 (March) 1935. (c) Kabat, H.; Magoun, H. W., and Ranson, S. W.: *J. Comp. Neurol.* **63**:211, 1936.

17. Hoff, E. C., and Green, H.: *Am. J. Physiol.* **117**:411, 1936.

18. Fulton, J. F.; Kennard, M. A., and Watts, J. W.: *Am. J. Physiol.* **109**:37, 1934.

19. Dusser de Barenne, J. G.: *Quart. J. Exper. Physiol.* **9**:355, 1915; *Proc. Roy. Soc., London, s.B* **96**:272, 1924.

In view of the conflicting results, a technic permitting direct stimulation of the uninjured hypothalamus under visual control is desirable, though the same certainty of localization can be obtained, more laboriously, with an adequate series of animals by the Horsley-Clarke apparatus and histologic control. The method presented here is simple and satisfactory.

METHOD

With the animal under light ether or pentobarbital sodium anesthesia the trachea is cannulated and the cat placed on a board with a special jaw clamp. The skin and the temporal muscle are reflected to expose completely one side of the skull, which is then removed by trephine and rongeur to lay bare the entire hemisphere, the longitudinal sinus being saved. The dura is then incised crucially and reflected over the cut edges of the bone, thus controlling bleeding. A thin, blunt strip (e. g., a forceps handle) is introduced into the longitudinal fissure and the exposed hemisphere pushed laterally to reveal the corpus callosum; the field is dried with long, thin, trimmed cotton pledgets wrung out after being soaked in Ringer's solution.

The entire left half of the brain is then removed with two strokes of a dull scalpel. The knife is inserted vertically in the midline until the point reaches the base of the skull. To avoid injury of the third ventricle, the head is previously rotated by means of the clamp, so that the point of the knife strikes about 5 mm. lateral to the midline. The blade is first swept forward, cutting all structures, and then backward and somewhat laterally, so that the brain stem is intact well above the colliculi. The result is incomplete hemidecerebration. At the end of the stroke, the brain is scooped out with the knife and the resulting cavity immediately plugged with cotton soaked in warm Ringer's solution. Considerable pressure is exerted on the cotton to compress against the bone the vessels at the base of the brain and thus stop bleeding. The animal shows little shock after this procedure.

When bleeding is stopped, ordinarily in a few minutes and with loss of only a few cubic centimeters of blood, the third ventricle is opened by wiping away the remaining sheet of tissue with cotton rolled into cigar-shaped pledgets, about 15 mm. long and 2 or 3 mm. thick, wrung out after soaking in Ringer's solution. These are held in a forceps and used as probes. With the choroid plexus as a landmark, the ventricle is best entered in the posterior region, and appears as a thin slit. The gray commissure or massa intermedia of the thalamus is then cut through with fine scissors; the remaining wall is wiped away, and the exposure is complete, down to the fine opening of the stalk of the hypophysis. Observations may begin almost immediately, for there is little shock. To permit free movement, the animal is suspended from a horizontal bar by means of towel clips hooked under the supraspinous ligaments near the pelvic and shoulder girdles, and into the skin and superficial muscles of the head.

Induced shocks from a Harvard inductorium were used, with 6 volts in the primary. Generally, definite responses were obtained with the secondary at from 10 to 12 cm., when the shocks could just be felt on the tongue. Tests were always begun with subminimal shocks, which were then increased until a definite response was obtained. A concentric electrode, made by pushing an enameled copper wire through an 18 gage hypodermic needle, with the final half inch bent at 75 degrees and the end cut off square, permitted well localized stimulation (referred to later). A barely visible extravasation marked the point of stimulation, so that accurate repetition was insured.

It must be emphasized that these stimuli were not excessive. As tested on an oscillograph, the long, closely approximated leads delivered only two thirds of the

voltage obtainable at the secondary terminals. Further, the shock strength with 6 volts in the primary and with the secondary at 12 cm. and tilted at 65 degrees is the same as that with 1.5 volts in the primary and the secondary at 12 cm. and in a horizontal position. Finally, the concentric character of the electrodes tends to concentrate the flow of current and minimize spread beyond the outer tube.

Respiration was measured with a tambour connected to a side arm of the tracheal cannula, and blood pressure, with a mercury manometer connected to the femoral artery. Bladder tone was obtained with a water manometer connected to a cannula inserted through the urethra and protruding into the lumen of the bladder, and stomach tone, with a manometer connected to a balloon in the stomach.

RESULTS

Two, or really three, areas on the wall of the third ventricle yielded sympathetic and motor responses on stimulation. A completely silent

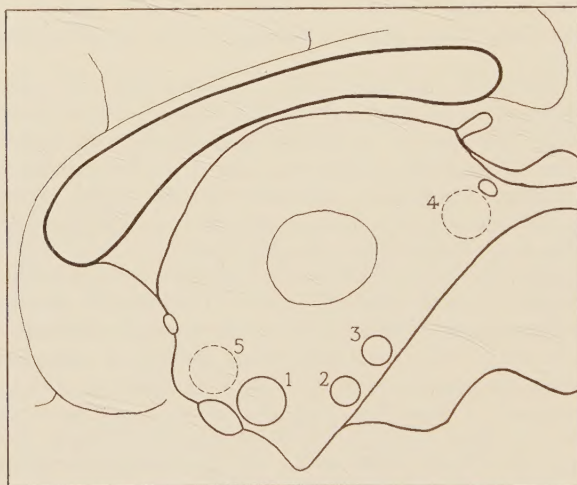


Fig. 1.—1 indicates the anterior area; 2, the rostral portion of the posterior area; 3, the caudal portion of the posterior area; 4, the area giving on stimulation the sum of responses from areas 1, 2 and 3, and 5, the area giving no response on stimulation alone, but causing inhibition of after-discharge following stimulation of areas 2 and 3.

region separated them. The anterior responsive region corresponded to the supra-optic and anterior hypothalamic nuclei, and the posterior pair, to the posterior hypothalamic nucleus. The intervening nonresponsive area corresponded to the infundibular nucleus, the hypothalamic periventricular nucleus and the dorsal median and ventral median hypothalamic nuclei (fig. 1). The nomenclature follows that of Ingram, Hannett and Ranson.²⁰

The anterior area (point 1, fig. 1), above the posterior border of the optic chiasm, is approximately 5 mm. in diameter, maximal responses

²⁰ Ingram, W. R.; Hannett, F. I., and Ranson, S. W.: *J. Comp. Neurol.* **55**: 333, 1932.

being elicited in all animals from the same central point and decreasing slightly to the periphery. A stimulus of threshold strength at the center was effective also at the periphery; so this gradation is not due to spread of the current. Also, the margin of the excitable area was sharp; moving the electrode less than 1 mm. abolished all response. The responses were a complex of motor and orthosympathetic activities and did not begin until a latent period of from two to four seconds had elapsed after the start of stimulation. Then there occurred: bilateral opening of the palpebral fissures, retraction of the upper and lower eyelids, protrusion of the eyeballs and marked dilatation of the pupils, respiratory and circulatory changes, contraction of the bladder and somatic movements.

The respiratory rate accelerated moderately—from 35 to 50 per minute—but the amplitude increased at least three times, so that the main effect was an increase in depth (fig. 2 *A*). The blood pressure rose sharply—on the average, 30 mm. of mercury. The high level was maintained about two seconds and then began to drop gradually, even if stimulation was continued. When stimulation ceased, there was a further slight drop, followed immediately by a marked rebound, with increases of from 25 to 30 mm. before the pressure finally fell to normal (fig. 2 *C*). Identical changes were found in curarized animals. No alteration of stomach tone was noted, but in about half the animals the urinary bladder contracted after a latency of from five to ten seconds.

No somatic movements of the limbs or back occurred, but the muscles of the neck showed a slight increase in tone, which resulted in some lifting of the head. Contraction of the facial and masticatory musculature gave an expression closely simulating rage or anger.

The posterior or supramamillary area, corresponding to the posterior hypothalamic nucleus, may be divided into a caudal and a rostral portion, each about 3 mm. in diameter. The responses obtained on stimulation of the caudal portion were mainly tonic, and those from the rostral portion, clonic.

Stimulation of the caudal portion (point 3, fig. 1) led to: bilateral retraction of the eyelids, pupillary dilatation and protrusion of the eyes; unilateral pilomotor erection on the ipsilateral side; tonic contraction of the respiratory muscles with stopping of respiration in inspiration, and a marked increase in blood pressure (averaging 30 mm. of mercury), which fell off before the end of stimulation. The blood pressure continued to fall after stimulation had ceased, and the heart rate often became slower as well. This is in sharp contrast with the vasomotor consequences of stimulating the anterior hypothalamic nucleus, which always left the circulatory system in seemingly better tone, with higher blood pressure and faster heart rate. Gastric motility was not changed, but in about half the experiments contractions of the bladder took place after from five to ten seconds.

The head and body were bent so as to produce a concavity directed toward the ipsilateral (stimulated) side; the ipsilateral limbs were flexed at all joints and the contralateral ones extended, and the tail was lifted. A facial expression appeared that can best be described as that of sham pain. The whole posture was strongly tonic and was held through the duration of the stimulus. When stimulation ceased, rhythmic running movements with all four limbs, lashing of the tail and panting began

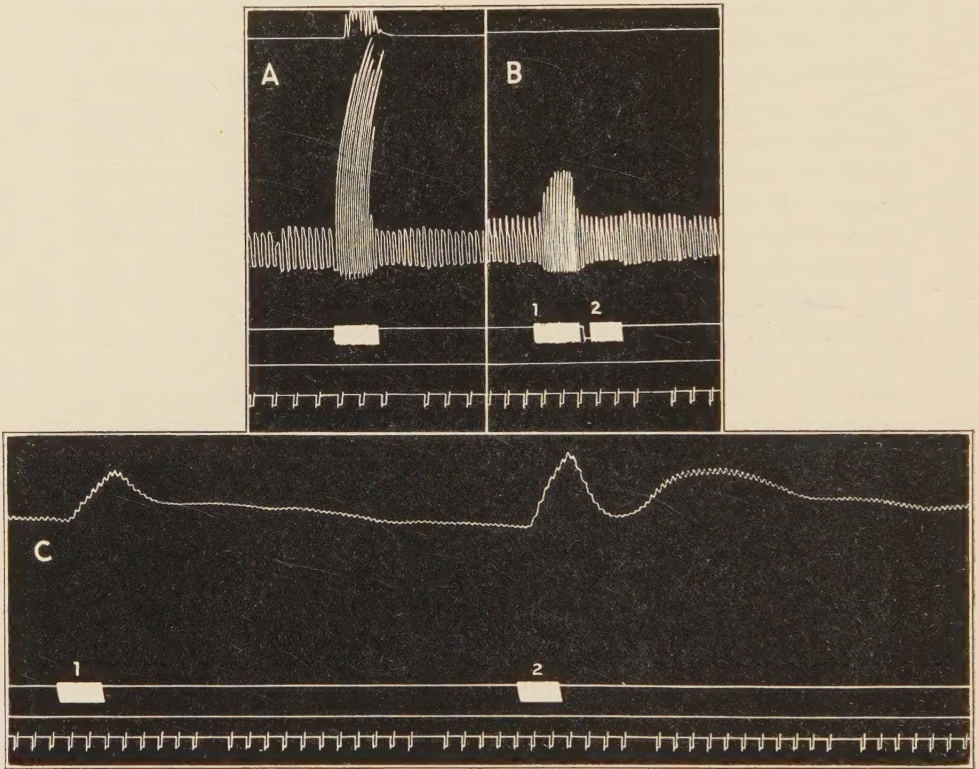


Fig. 2.—*A* shows increase in the depth of respiration on stimulation of the anterior hypothalamic nucleus (point 1 of figure 1); *B*, increase in the speed of respiration on stimulation of the posterior hypothalamic nucleus of the same animal (1 indicating stimulation of point 2 of figure 1, and 2, stimulation of the supra-optic region), and *C*, increases in blood pressure, with the mercury manometer connected to the right femoral artery. 1 indicates stimulation of the posterior hypothalamic nucleus (point 2 of figure 1), and 2, stimulation of the anterior hypothalamic nucleus (point 1 of figure 1).

promptly and lasted up to five minutes. This after-effect is exactly similar to the somatic movements occurring during stimulation of the rostral portion of the posterior region.

Stimulation of the rostral portion of the posterior area (point 2, fig. 1) led to the same optic, pilomotor and bladder responses as did stimulation of the caudal portion. The blood pressure was also increased, to like extent with and without curare. Respiration was markedly accelerated, from an average rate of 35 to one of 65 per minute, but the amplitude of movements was only slightly increased (fig. 2*B*). The nares, face and tongue made small movements synchronous with respiration, giving an appearance of panting. This marked increase in rate is in contrast with the response on stimulating the anterior nucleus, which was mainly an increase in amplitude.

The head was rotated on the longitudinal axis, with the snout directed to the stimulated side; the back was bent, with the concavity directed toward the same side; the limbs showed walking or running movements accompanied by lashing of the tail, and a facial expression of sham fear appeared. These phenomena did not cease or alter after stimulation ended but continued for some time, in one case seven minutes.

The running movements, both during and after stimulation, could be changed by peripheral stimulation. Pinching any part of the body stopped the limbs in extension. Light touch on the plantar surface of the foreleg, however, caused the leg to stop at once in any position and led to marked flexion of the toes which resembled a grasping movement; similar stimulation of the dorsal surface of the moving limb changed the pattern of the movement so that the leg stepped accurately over the obstruction. If the lashing tail came into contact with a foreign object, it ceased to wave but curled around the object and tended to grasp it.

Stimulation of the preoptic and supra-optic regions (point 5, fig. 1) alone had no effect, but promptly and completely inhibited the after-effect of stimulation of the posterior hypothalamic regions. The panting and running movements stopped, and the facial expression of fear disappeared. Stimulation of the thalamic surface of the third ventricle gave no response; stimulation of the pretectal region led to constriction of the pupils and closing of the eyelids, and that of the anterolateral wall of the aqueduct of Sylvius (point 4, fig. 1), to strong running movements with increase in the blood pressure and panting.

All the responses described were obtained alike with the animal under light ether and under pentobarbital sodium anesthesia. Increasing depth of anesthesia diminished all the responses and finally abolished them in regular order. The somatic changes disappeared first, then those of respiration and finally the vasomotor and pupillary responses. The latent period, from two to four seconds, was as long for the somatic as for the sympathetic responses.

In all cases, pushing the electrode into the ventricular wall a millimeter or two abolished the response obtained from the surface. This,

plus the sharp lateral limits of excitable regions, is evidence of the limited spread of current in these experiments and of the localization of excitable masses. No noticeable injury was produced by stimulation, since, even after very strong shocks, the same responses could be obtained repeatedly hour after hour.

COMMENT

My findings show clearly the existence of diencephalic centers of autonomic and somatic motor character. Further, there is definite localization of function as between the anterior and the posterior region of the lower part of the wall of the third ventricle. The somatic and the autonomic responses are obviously related. Both appear together after the same latency and are of a character appropriate to each other. Thus, from the anterior region the facial expression of rage is evoked with its autonomic and respiratory concomitants, while from the posterior region are obtained the manifestations of fear or pain. Such integrated behavior strongly indicates that these observations are physiologically valid, due to stimulation of functional units, rather than a potpourri of effects resulting from the excitation of independent structures accidentally associated in the path of a spreading current.

The respiratory changes—predominant increase in amplitude from the anterior portion of the hypothalamus and in rate from the posterior portion—are in harmony with the results of Crouch and Elliot,²¹ who stimulated the same regions with the aid of the Horsley-Clarke apparatus. Otenasch and Lilienthal²² showed, by successive transections, that panting movements persisted when the anterior portion of the hypothalamus was removed but the posterior portion remained—further evidence of the existence of separate centers controlling rate and amplitude. Bogen²³ offered evidence that there are chemically distinct controls for the rate and the depth of respiration.

Despite some negative findings (Leiter and Grinker²⁴), there is now general agreement on the existence of vasomotor centers in the hypothalamus (Karplus and Kreidl;¹² Beattie;^{13b} Ranson, Kabat and Magoun,^{16b} and Crouch and Elliot²¹). Separation of the effects of stimulation of the anterior and those of the posterior region, such as are presented here, has not previously been demonstrated clearly. Pupillary changes following hypothalamic stimulation have been studied most

21. Crouch, R. L., and Elliot, W. H., Jr.: *Am. J. Physiol.* **115**:245, 1936.

22. Otenasch, F. J., and Lilienthal, J. L.: *Am. J. Physiol.* **116**:117, 1936.

23. Bogen, E.: *Am. J. Physiol.* **85**:352, 1928.

24. Leiter, L., and Grinker, R. R.: *Role of Hypothalamus in Regulation of Blood Pressure: Experimental Studies, with Observations on Respiration*, *Arch. Neurol. & Psychiat.* **31**:54 (Jan.) 1934.

recently by Ranson and Magoun,²⁵ and contraction of the urinary bladder, by Ranson, Kabat and Magoun^{16b} and Kabat, Magoun and Ranson.^{16c} My observations are in harmony with theirs.

Karplus and Kreidl¹² and Ranson and his co-workers^{16b} on stimulating the hypothalamus obtained sympathetic responses throughout its length and inclined to the view that the most anterior responding region was the sympathetic center and that its efferent tract was engaged more caudally. The present findings suggest rather the existence of several discrete centers in the hypothalamus, distributed anteroposteriorly, the tracts of which become associated only more posteriorly. At least, on stimulation of the wall of the aqueduct as it leaves the third ventricle (point 4, fig. 1) there results a mixture of the various responses obtained discretely from the separate, more anterior regions. Respiration, for example, is markedly increased in both rate and amplitude. Incidentally, the presence of several centers giving qualitatively discriminate responses in which somatic and autonomic effectors cooperate indicates for the hypothalamus a "higher" rôle than that of a center for a general and indiscriminate orthosympathetic discharge in emergencies (Cannon²⁶).

Further, Ranson has assigned a lateral position to the hypothalamic sympathetic center. Responses from medial regions, where I find them, he attributed to stimulation of tracts crossing in the supramamillary and supra-optic decussations. In fact, my anterior region is, almost surely, the supra-optic commissure in which Kabat, Magoun and Ranson²⁷ and Kabat²⁸ found activity to the midline. Their more posterior reactive region may also correspond to mine, since like effects resulted from stimulation. It is significant, however, that tracts are mainly gathered laterally and centers more medially; so, although I have not explored the lateral portion of the hypothalamus adequately, I incline to the reverse interpretation.

Somatic motor responses from the hypothalamus have been previously observed and variously interpreted. Struggling movements on stimulation occurred in the experiments of Ranson and his co-workers^{16b} after a longer latency than that for the sympathetic effects, and were interpreted as due to a separate system not related to the hypothalamus. In my experience, the two were always closely associated.

25. Ranson, S. W., and Magoun, H. W.: Respiratory and Pupillary Reactions Induced by Electrical Stimulation of Hypothalamus, *Arch. Neurol. & Psychiat.* **29**:1179 (June) 1933.

26. Cannon, W. B.: Bodily Changes in Pain, Hunger, Fear and Rage, ed. 2, New York, D. Appleton & Company, 1929.

27. Kabat, H.; Magoun, H. W., and Ranson, S. W.: Electrical Stimulation of Points in Forebrain and Midbrain: Resultant Alterations in Blood Pressure, *Arch. Neurol. & Psychiat.* **34**:931 (Nov.) 1935; footnote 16c.

28. Kabat, H.: *J. Comp. Neurol.* **64**:187, 1936.

The acute experiments of Hinsey, Ranson and McNattin²⁹ proved that the posterior portion of the hypothalamus must be intact for locomotion, since its destruction leads to disturbed equilibrium and failure of the walking mechanism. Bard,¹¹ likewise, found that the chronic diencephalic cat could walk, run and express rage in a manner impossible to the decerebrate animal. I also observe walking and running movements on stimulation of the posterior portion of the hypothalamus alone. Besides coordinated movements, with their tonic concomitants, maintained tonic postures are also elicited from the hypothalamus. These are analogous to the tegmental reaction described by Ingram and his co-workers³⁰ in the mesencephalon and probably represent tonic components of standing. Cutaneous stimulation of the plantar aspect of the foot during this response induces a flexor movement of the toes, and similar stimulation of the tail causes it to curl around the stimulating object. Such findings strongly suggest a localized center for postural locomotion and for grasping. The hypothalamus, like frontal areas 4 and 6 (Fulton, Kennard and Watts¹⁸), thus seems to be both sympathetic and motor. Whether the frontal lobe has autonomic properties by virtue of connections with the hypothalamus or the hypothalamus manifests motor properties via connections with the cortical or subcortical motor systems or both regions have direct motor and sympathetic connections with the lower neuraxis remains to be determined.

SUMMARY

A method is described of stimulating the lateral wall of the third ventricle of the hemidecerebrate cat under direct visual control. Stimulation reveals several distinct autonomic and somatic motor centers and one inhibitory "center." An anterior hypothalamic (supra-optic) nucleus gives optic, respiratory, circulatory and somatic responses suggestive of rage; the rostral part of a posterior region, those of fear, and its caudal part, those of pain. Stimulation of the anterior region increases the depth of the respiration and, both immediately and for longer periods, the blood pressure. Stimulation of the posterior region increases the respiratory rate and, after a temporary rise, lowers the blood pressure. Somatic effects are obtained almost exclusively from the posterior region—characteristic tonic postures (grasping) during stimulation of its caudal portion, and coordinated running, stepping and other movements during and after stimulation of the rostral portion and after stimulation of the caudal part.

I wish to thank Drs. Leon Ectors and R. W. Gerard for their aid in this work.

29. Hinsey, J. G.; Ranson, S. W., and McNattin, R. F.: *Tr. Am. Neurol. A.* **55**:128, 1929.

30. Ingram, W. R.; Ranson, S. W.; Hannet, F. I.; Zeiss, R., and Terwilliger, E. H.: *Results of Stimulation of Tegmentum with Horsley-Clarke Stereotaxic Apparatus*, *Arch. Neurol. & Psychiat.* **28**:513 (Sept.) 1932.

